

THE *CHYMOMYZA ALDRICHII* SPECIES-GROUP
(DIPTERA: DROSOPHILIDAE): RELATIONSHIPS, NEW
NEOTROPICAL SPECIES, AND THE EVOLUTION OF
SOME SEXUAL TRAITS

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Abstract.—Seven new species of *Chymomyza* are described: *C. diatropa*, *C. exophthalma*, *C. guyanensis*, *C. jamaicensis*, *C. microdiopsis*, *C. mycopelates*, and *C. procnemolita*. *Chymomyza maculipennis* Hendel is a junior synonym of *C. bicoloripes* (Malloch). Genitalia of male and female *C. bicoloripes* and male *C. albitarsis* (Hendel) are described and those of *C. aldrichii* Sturtevant and *C. procnemoides* Wheeler are figured. A key is provided for the identification of all members of the *Chymomyza aldrichii* species-group. Males of 5 species have conspicuously broadened heads. Synapomorphy distributions suggest that this trait evolved independently twice, in quite different manners. Spines on the male prothoracic femora evolved less dramatically and have been lost in *C. bicoloripes* and *C. mesopecta* Wheeler. Rampant homoplasy in adult morphology, however, obscures the phylogenetic relationships somewhat and limits definitive statements on the origins of extreme sexual dimorphism in these flies.

Chymomyza Czerny is an undoubtedly monophyletic genus in Drosophilidae based on its many synapomorphies, which were reviewed by Okada (1976). Some of these traits are a proclinate orbital bristle that is situated medial to and between the 2 reclinate, an ov scape with fine setae, male terminalia with prominent gonopods and ventral epandrial lobes, and the males possess strong spines on the ventral surface of the prothoracic or mesothoracic femora. The genus is worldwide in distribution. It is considered one of the advanced genera of Drosophilinae (the Steganinae being the other, but primitive, subfamily), and perhaps originated from *Drosophila* (*Sophophora*) stock in Africa with its sister-group, *Neotanygastrella* (Throckmorton, 1975). Some 43 species are presently known, and many of these were only recently described (Okada, 1976, 1981). Still, in comparison to some other "natural" genera such as *Leucophenga* (158 spp.), the group is dwarfed. Okada (1976) divided *Chymomyza* into the *obscura*, *fuscimana*, *costata*, *procnemis*, and *aldrichii* species-groups, the last 2 being close relatives.

Hendel (1917) described the first neotropical member of the *aldrichii* species-group, and, at that time, it was the second known instance at the generic level of a broad-headed drosophilid male. *Zygothrica dispar* (Wiedemann) (originally as *Achias*) was the species first described with a superficially similar trait. Because of its unusual head shape, Hendel (1917) erected *Zygodrosophila* to ally the specimen with *Drosophila* and with *Zygothrica*. Duda (1927) recognized that "*Zygodrosophila*" *albitarsis* Hendel was probably a *Chymomyza* based only on Hendel's description. In the catalogue of the world Drosophilidae (Wheeler, 1981), *Z. albitarsis* is placed under *Chymomyza*, but an explicit synonymization of *Zygodrosophila* has not been done.



Fig. 1. Habitus, anterolateral view, male *Chymomyza microdiopsis*, n. sp.

Duda (1927) described *C. laevilimbata* and Malloch (1926) described *C. bicoloripes* (as *Drosophila*). In 1936, Hendel described *C. maculipennis*, but Wheeler (1957) mentioned that *C. maculipennis* is probably synonymous with *C. bicoloripes* judging from Hendel's description. Sturtevant (1921) discovered 2 new species with broad heads from Haiti and from British Guyana, but he deferred their descriptions because, as he wrote (p. 61), "it seems better to wait for a study of the male genitalia before attempting to determine the specific limits in the section of the genus to which they belong." Wheeler (1968) described *C. mesopecta*, an unusual member of the species-group, which I will treat here only briefly.

METHODS

Assistance from the following individuals in providing specimens is appreciated (their respective institutions are abbreviated in parentheses and are referred to in the descriptions): Daniel Bickel, Museum of Comparative Zoology, Cambridge, Mas-

sachusetts (MCZ); Ruth Contreras-Lichtenberg, Vienna Natural History Museum (NHMW); Wayne Mathis, Smithsonian Institution, Washington, D.C. (USNM); J. Frank McAlpine, Canadian National Collection, Ottawa (CNC); Kathleen Schmidt, American Museum of Natural History, New York (AMNH). Brian H. Cogan, at the British Museum (Natural History), Paul H. Arnaud, Jr. (California Academy of Sciences, San Francisco), and Francisca Val (Museu de Zoologia de São Paulo) kindly checked through the drosophilids in their respective collections for *Chymomyza*. Throughout the text CUIC denotes Cornell University Insect Collections as a depository. The holotypes of *C. bicoloripes*, *C. albitarsis*, *C. procnemoides*, and *C. maculipennis* were studied.

For all species the male and, where available, female terminalia were prepared by clearing them in 10% KOH, washing them in warmed distilled water, passing them through 70% ethanol and then glycerine, and mounting them in glycerine jelly. A Leitz Nomarski optics microscope with camera lucida was used to illustrate most structures. Scanning electron micrographs of the male prothoracic femora were taken at 550 $\times$ magnification with 5 kV beam current. Specimens were gold-palladium sputter-coated. Several standard measurements were made and some ratios also taken: for the wing, measurements are indicated in Figure 14; those for an analysis of head shapes are given in the discussion section.

Relative phylogenetic relationships are hypothesized based on sets of synapomorphies. Hence, no hypotheses of ancestral relationships are given here. *Chymomyza amoena* (Loew), which belongs to the *fuscimana* species-group (sensu Okada, 1976), was used as an outgroup for deciding the polarity of character states. For some quantitative characters discontinuous states were distinguished where there was an obvious (and, so, probably statistically significant) gap in a morphocline.

My use of morphological terms follows conventions established by McAlpine (1981). This departure from standard *Drosophila* taxonomy is needed to standardize terms for dipterists, but especially for homologizing structures in the terminalia (see Fig. 4). The alternative term paraphysis was used for "paramere" (sensu Griffiths, 1972, 1981) because the latter is a term coined by coleopterists for paraphallic processes at the base of the aedeagus and it is unclear if the 2 structures in beetles and flies are homologous. Oviscape is used here in place of terms in the *Drosophila* literature that refer to the modified lateral surfaces of sternite 8 in females ("egg guides," "ovipositor plates," . . .). It is more specific than "egg guide," which can also refer to the eversible membrane posterior to sternite 8 that often bears fine scales in some drosophilids and actually channels the egg into spaces. "Ovipositor plates" suggests the sternites to be true orthopteroid-type ovipositors, which are appendicular in origin.

All measurements are in millimeters.

RESULTS

I. Species-group diagnosis.

The arista has usually 3 dorsal and 2 ventral branches. The frontal vitta is very finely striate with marks running anteroposteriad, and is golden yellow. Shiny glabrous fronto-orbital plates border the frontal vitta. Eyes are sparsely pilose and brick red. Variable degrees of head broadening in the males of some species occurs, the extent

and manner of which is described later. A glabrous ocellar triangle is dark brown to black in the area bordered by the ocelli. The prothoracic coxae and trochanters are relatively light in comparison to the general body color (they are usually white or off-white), and the prothoracic femora, tibiae, and basitarsi are contrastingly dark brown to black. The remaining tarsal segments, 2–5, are white. Meso- and metathoracic legs are similar in color to the body ground color. The entire basicostal, costal, and variable portions of the proximal end of the subcostal cell are infuscated dark-brown to black. The costal vein and usually R_{2+3} and R_{4+5} are much darker than the other veins.

Abdominal tergites are shiny black, and each possesses 3–4 rows of fine long setae arranged transversely. Terminalia are very diagnostic and can be polymorphic, especially for the males. Male terminalia are large and, when not retracted into the eighth abdominal segment, are usually slung ventrally in the manner of many dolichopodids. The aedeagus is prominent, bilaterally symmetrical and compressed, particularly the distiphallus, which is usually bulbous in lateral view compared to the rest of the aedeagus. The oviscapae and spermathecae do not appear distinctive among other *Chymomyza* groups, although they can vary among species. Neotropical members of the group are generally quite small, being about $\frac{1}{2}$ the size of some common nearctic species such as *C. amoena* (Loew) and *C. aldrichii* and they resemble in habitus the North American species *C. procnemoides*. Very little sexual dimorphism in size exists; in 3 of the species (*C. guyanensis*, n. sp., *C. exophthalma*, n. sp., and *C. procnemolita*, n. sp.) females are about 10% larger than the males.

II. Key for the identification of males and, where applicable, females of the *Chymomyza aldrichii* species-group members. Final identification often requires examination of some microscopic features of the male and female terminalia (see Figs. 2–12, 13a–h).

1. Entire body dark brown to black 2
 - Ground color of head and thorax yellow-orange to light brown 3
2. Eight rows acrostichal setulae present; North America *aldrichii*
 - Six rows acrostichal setulae present; South and Central America *laevilimbata*
3. Femoral spines of male prothoracic legs absent (Fig. 15a); South America 4
 - Femoral spines of male prothoracic legs present (Figs. 15b–h) 5
4. Males femoral spines only on mesothoracic legs *mesospecta*
 - Male femoral spines absent on pro- or mesothoracic legs; crossveins dm-cu infuscated (Fig. 14B) *bicoloripes*
5. Ventral lobe of male epandrium with apex broader than the length of the lobe (Fig. 12); spermatheca having scale-like exterior (Fig. 13g); North America *procnemoides*
 - Not with above characteristics; all neotropical forms 6
6. Face with a distinct, dark brown border on the anterior margin (Fig. 17); male eyes ventrally elongate, or variable for this trait 7
 - Face unicolorous yellow, with no distinct dark marking on anterior margin of the face 8
7. Pleura brown; male distiphallus strongly hooked (Fig. 4); Jamaica *jamaicensis*
 - Pleura similar in color to the yellow-orange notum; male terminalia variable but always with a club-shaped gonopod bearing 2 strong, lateral setae (Fig. 3); distiphallus round-ed; widespread in Central and South America *diatropa*

8. Male head obviously broadened (Fig. 17) 9
 - Male head width the same or only slightly broader than that of thorax 11
9. Head broadening due to ventral expansion of eyes (as in *C. diatropa*, *C. jamaicensis*: Fig. 17); distiphallus apically truncate (Fig. 7); known only from a single male from Paraguay *albitarsis*
 - Male heads broadened by an expansion of the fronto-orbital and parafacial plates; distiphallus apically rounded 10
10. Anterior reclinate orbital seta below line extending across dorsal margin of scape; 2 rows of profemoral spines undifferentiated (Fig. 15d); hypandrium uncleft, cercus strongly pointed (Fig. 2); Cuba *microdiopsis*
 - Anterior reclinate orbital situated above line extending across dorsal margins of scapes; ventral row of male profemoral spines shorter and thinner than those in medial row; cercus rounded (Fig. 10); Panama to Peru, Trinidad *exophthalma*
11. Six to 7 rows acrostichal setulae present; proclinate orbital setae end lateral to middle of pedicels (Fig. 17) *mycopelates*
 - Eight rows acrostichal setulae present; proclimates end at middle of pedicel (Fig. 17) 12
12. Nine to 11 prensisetae on surstylus; setae on ventral lobe of epandrium are relatively short (Fig. 8); distiphallus without a lateral knob *guyanensis*
 - Seven to 8 prensisetae on surstylus; ventral lobe of epandrium with long apical setae; distiphallus with a lateral knob (Fig. 5) *procnemolita*

III. Species descriptions. The order in which they are presented here reflects their phylogenetic positions (Fig. 16).

The *mycopelates* lineage
Chymomyza mycopelates, new species
 Figs. 11, 13e, 15h, 17

Description. Head light brown, frons and face glabrous. Light brown on oral margin of face near eyes. Three dorsal and 2 ventral arisal rays, flagellomere I light brown. Lunule and surrounding region dull, light yellow. Eyes bare. Well-developed vibrissa present, subtended by 5–6 setae decreasing in size posteriad. One genal and 1 subgenal seta present. Anterior reclimates above line extending across dorsal margin of pedicels. Proclimates closer to anterior reclimates than to posterior reclimates. Inner verticals and posterior reclimates longest setae on head; anterior reclimates and proclimates shortest. Fronto-orbital plates not extended beyond middle of pedicel. Anterior reclinate, posterior reclinate and inner vertical setae on each side of head in line with each other. Posterior reclinate $\frac{1}{2}$ the distance between anterior reclinate and inner vertical. Head width to total thorax length ratio (HW/ThL) = 0.80 (5♀), 0.83 (5♂), total thorax length (ThL) = 0.81 (5♀), 0.83 (5♂).

Notum and pleura light orange, but darker to almost light brown on subscutellum and katapisternum. Sternum light yellow to off-white. A mean of 10 (range: 8–13) spines in medial row and 11 (9–13) in the ventral row of male prothoracic femora. Medial row spines about $\frac{3}{4}$ the length of the other spines. Forecoxa with 5 prominent distal setae. One postpronotal seta present; pair of lateral prescutellar setae about twice the length of acrostichal setulae. Dorsocentral setae and anterior scutellars in line with each other. Wing measurements: C.I. = 1.03 (5♂ + 5♀); 4-V index = 2.55 (5♀), 2.73 (5♂); 4-C index = 1.75 (5♀), 1.89 (5♂).

Female with narrow, somewhat elongate ov scape possessing 4 terminal setae and row of evenly spaced setae (usually 6) on ventral margin. Spermatheca large and conspicuously ribbed on basal third of the capsule. An introvert extended about 0.8 the capsule length, and an inconspicuous apical indentation present. Male genitalia conspicuously unique: cercus small and evenly rounded in profile, epandrium high, its length less than $\frac{1}{2}$ its height. Inner wall of epandrium bears 3 straight, fine setae. Surstylus with 8 prensisetae, all rather short. Ventral epandrial lobe narrowed apically, setae on apical quarter of lobe short and fine (about 20 present). Ventral margin of lobe bearing a row of 20–25 very long setae, their length 3 times or more the lobe width. Epandrial lobe bearing sparse vestiture of microtrichia on base. Ventral margin of hypandrium strongly cleft; paraphysis indistinct, bearing 3 short sensilla. Gonopod of moderate size and with 1 strong, dorsally projecting, scale-like seta situated preapically and 4 finer ones of equal length evenly spaced on dorsal margin. Distiphallus curved upward, with lateral knob and a thinner one on ventral margin. Apex of distiphallus membranous and can appear torn: it, like that of *C. guyanensis*, probably eversible. No vestiture present on distiphallus. Main shaft of endophallus very thin, its width about $\frac{1}{3}$ that of ventral epandrial lobe. Aedeagal apodeme rudimentary and bearing no lateral flanges: attached to a broadly triangular gonopodal apodeme.

Holotype. ♂, COSTA RICA: La Francia, XI-14-52, Goodyear Plantation, J. B. Carpenter (USNM). Additional label: "feeding on fungus *Ceratostomella fimbriata* on fresh cut logs of *Hevea brasiliensis*."

Paratypes. 24♂♂ and 9♀♀, same locality and date as the holotype (all USNM).

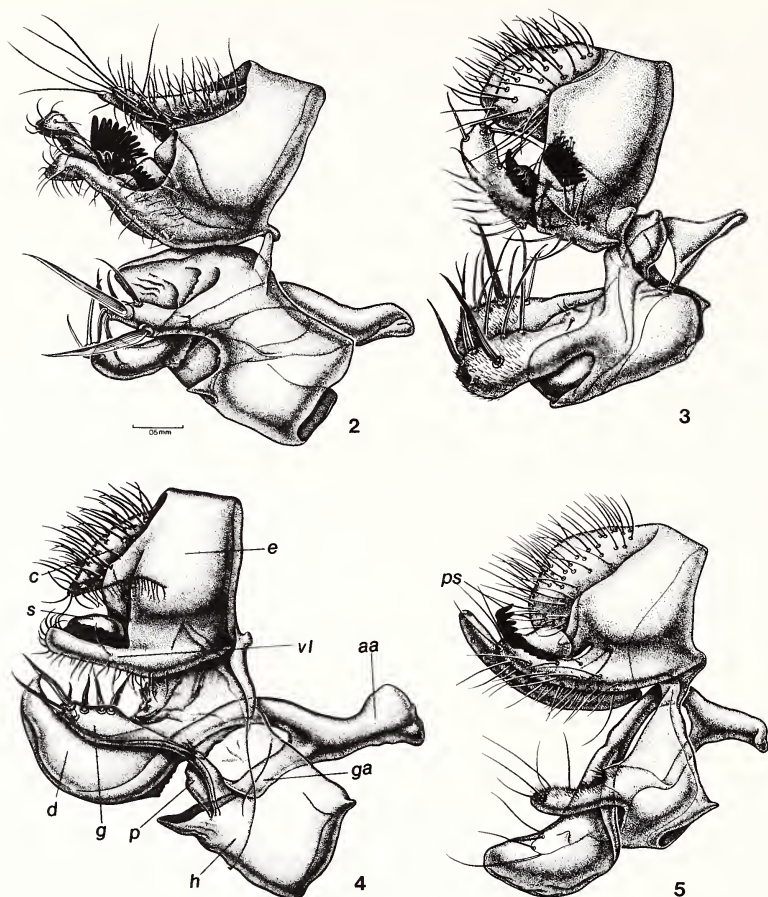
Etymology. Gr., "fungus-approacher," because of its feeding habit.

***Chymomyza microdiopsis*, new species**

Figs. 1, 2, 13f, 14C, 15d, 17

Description. Head and thorax light orange, ventral portions of head light yellow to almost white. Four dorsal and 2 ventral arisal branches. A vibrissa each subtended by 5–7 setae of equal length. Proclinate orbital setae end at middle of pedicel. Anterior reclinate, posterior reclinate and inner verticals in line with each other. Anterior reclinates attached at level of anterior margin of scape. Inner verticals longest setae on head and ocellars are shortest. HW/ThL = 1.38 (10♂♂). One large postpronotal seta and 6 rows of acrostichals. Forecoxa with 6 (5–8) strong, equal-sized setae distad. Eight to 10 (mean of 9) spines per row on male prothoracic femora. Mesothoracic coxa with 5 setae, metathoracic coxa with 1. ThL = 0.83 (10♂♂), 0.98 (1♀). Wing measurements: C.I. = 1.18 (10♂♂, 10♀♀), 4-V index = 2.73 (10♂♂), 4-C index = 1.78 (10♂♂).

Ov scape narrowed apicad, with 5 long apical setae and 3 shorter ones. Hypoproct modified internally into a pair of broadened flanges. Spermatheca of intermediate size (about 60 μ m); an introvert present. Spermathecal capsule with smooth surface. Male cercus apically pointed and with 2 very long apical setae. Ventral lobe of epandrium apically knobbed, with 10–12 setae. Surstylus with usually 10 prensisetae, sometimes 11; many fine setae on medial surface of lobe. Dorsal margin of epandrium narrow in profile, hypandrium large. Paraphyses small and with 3 short, fine sensilla. Gonopod with 2 large scale-like setae and 4 smaller, apical ones. Gonopod devoid of microtrichia. Distiphallus narrow in profile, apically rounded, ventral margin with



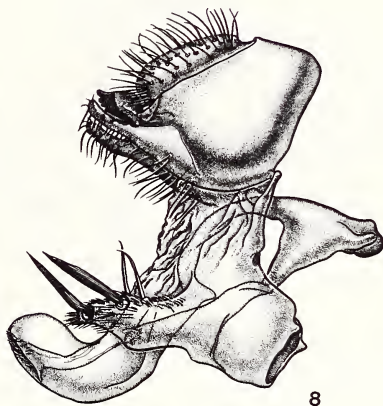
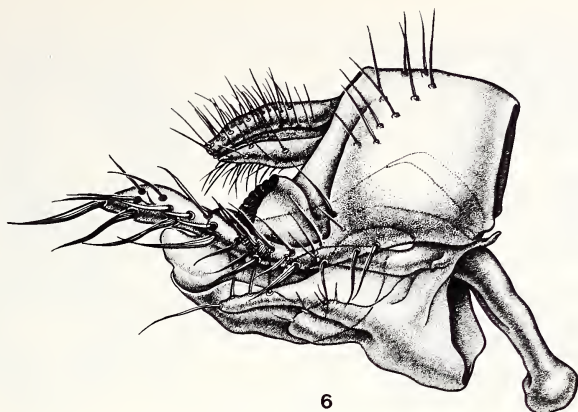
Figs. 2-12. Male terminalia of *Chymomyza aldrichii* species-group members, lateral view, all to the same scale. 2. *C. microdiopsis*. 3. *C. diatropa*. 4. *C. jamaicensis*. 5. *C. procnemolita*. 6. *C. bicoloripes*. 7. *C. albitarsis*. 8. *C. guyanensis*. 9. *C. aldrichii* (ventrolateral view of hypandrium and associated appendages). 10. *C. exophthalma*. 11. *C. mycopelates*. 12. *C. procnemoides*. Abbreviations: aa, aedeagal apodeme; c, cercus; d, distiphallus; e, epandrium; g, gonopod; ga, gonopodal apodeme; h, hypandrium; p, paraphysis; ps, prensisetae; s, surstylus; vl, ventral epandrial lobe.

approximately 8 blunt serrations along length with a larger knob anteriad. Basiphallus of medium height; lateral flanges well-developed on aedeagal apodeme. Apex of distiphallus devoid of microtrichia.

Holotype. ♂, CUBA: Santa Clara Province, San Juan Mountains, Jan.-Feb. 1927, C. T. and B. B. Brues (USNM).

Paratypes. 11♂♂ (MCZ), 15♂♂ and 1♀ (USNM), all with same label data as holotype.

Etymology. Gr., "tiny diopsid," after its most striking feature that is common in a distantly-related family.

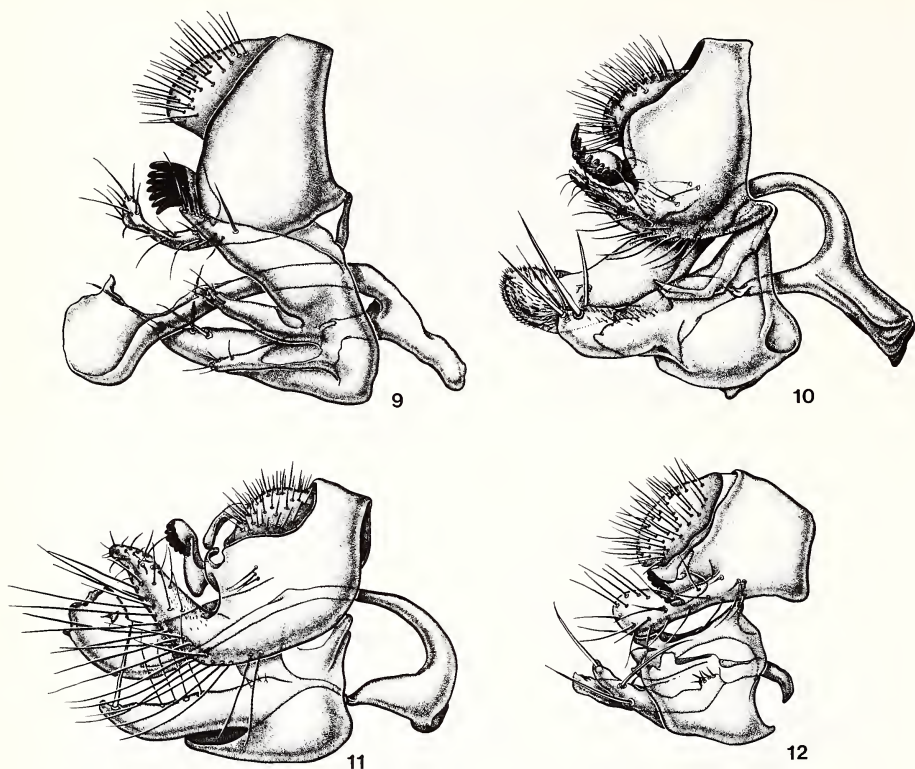


Figs. 6–8. See caption on page 348.

***Chymomyza exophthalma*, new species**

Figs. 10, 13h, 17

Description. Head yellow, with no conspicuous markings. Male head variably broadened due to expanded fronto-orbital and parafacial plates. Inner margins of eyes parallel and not divergent dorsally. Three dorsal and 2 ventral arisal branches, the third dorsal one very close and just distal to first ventral one. Proclimates ending just mediad of pedicel center and their bases lying equidistant between anterior and posterior reclimates. Anterior reclimates in line with dorsal margins of scapes. Inner vertical medial to line extending from anterior to posterior reclimates. Inner verticals the longest head setae. Fifteen to 17 postocular setae per side. Postocellars relatively long, lengths about that of paraverticals. A heavy vibrissa subtended on each side



Figs. 9-12. See caption on page 348.

by 4 shorter setae of equal thickness. One genal and 1 subgenal seta. HW/ThL = 1.07 (5♂♂), 0.90 (5♀♀).

Thorax, particularly pleura and sterna, darker than head. Subscutellum light brown. Six rows evenly spaced acrostichals. One postpronotal seta, the length of the 2 lateral prescutellars about twice that of acrostichals. Dorsocentrals and anterior scutellars in line with each other. Prothoracic coxa with 4-5 heavy, long setae distad; also several long, finer setae. Male prothoracic femur with 9-10 spines in medial row, their lengths about equal to $\frac{3}{4}$ femur width. Seventeen shorter spines in ventral row. Twelve fine setae in lateral row bordering the ventral pollinosity. Mesothoracic coxa with 2 long setae and metathoracic with 1. Metathoracic tibia brown, but not as dark as fore femora and also gradually lighter distad. Wing measurements: C.I. = 1.16 (5♂♂), 1.28 (5♀♀); 4-V index = 2.40 (5 ♂♂), 2.48 (5♀♀); 4-C index = 1.65 (5♂♂), 1.55 (5♀♀).

Spermatheca trapezoidal in profile to almost oval, base abruptly funneled. Apical indentation inserted into open apex of introvert. Oviscape long and with 5 long and 2 shorter apical setae. Introvert slightly ribbed. Male terminalia similar to those of *C. procnemolita* except for following characteristics: 11 prensisetae per surstylus; 4 long fine setae on inner wall of epandrium; ventral lobe of epandrium apically pointed

and setae on it diminished in length apicad; dense microtrichia on distiphallus; 2 sensilla on prominent, pointed paraphysis; paraphysis attached proximad to a sclerotized, sharp lobe; gonopod about as high as distiphallus and with 2 prominent, thick setae and 3 thinner ones; gonopodal apodeme separated from main endophallal shaft by wide curvature; aedeagal apodeme robust and as long as ventral margin of hypandrium. Like *C. procnemolita*, distiphallus with a lateral knob, an uncleft hypandrial margin, a rounded cercus, and the distiphallus of a similar shape.

Holotype. ♂, PANAMA: Canal Zone, Barro Colorado Island, 26 May 1961, S. B. Pipkin (USNM).

Paratypes. PANAMA: Canal Zone, Barro Colorado Island, 19–26 May 1961 (4♂♂, 4♀♀) and 10 May 1961 (1♀), 10 September 1960 (1♀), S. B. Pipkin (all USNM). PERU: Madre de Dios, Rio Tambopata Reserve, 30 km SW Puerto Maldonado IX/19–X/10/84, 12°12'S, 69°16'W, 290 m, D. A. Grimaldi (2♂♂, 2♀♀) (CUIC). TRINIDAD: Arima, 800–1,200 ft, 10–22 Feb. 1964, J. G. Rozen & P. Wygodzinsky (3♂♂, 2♀♀) (AMNH).

Etymology. Gr., “bulging-eyed,” in reference to the frontward appearance of the head.

Comments. Some behavioral notes were taken on this species and are given in the discussion section under Leg Ornamentation and Reproductive Behavior.

The *diatropa-guyanensis* lineage

Chymomyza bicoloripes (Malloch, 1926), **New Combination**

Figs. 6, 13a, 14B, 15a

Drosophila bicoloripes Malloch, 1926:31. Holotype: ♂, PANAMA: Canal Zone. Las Cascadas. A. H. Jennings, coll. Type no. 28467 (USNM).

Chymomyza maculipennis Hendel, 1936:7. Holotype: ♀, BRAZIL: Amazonas-Dampfer, Gurupa-Almeirim, 29.V.27, Zerny. (NHMW). **New Synonymy**.

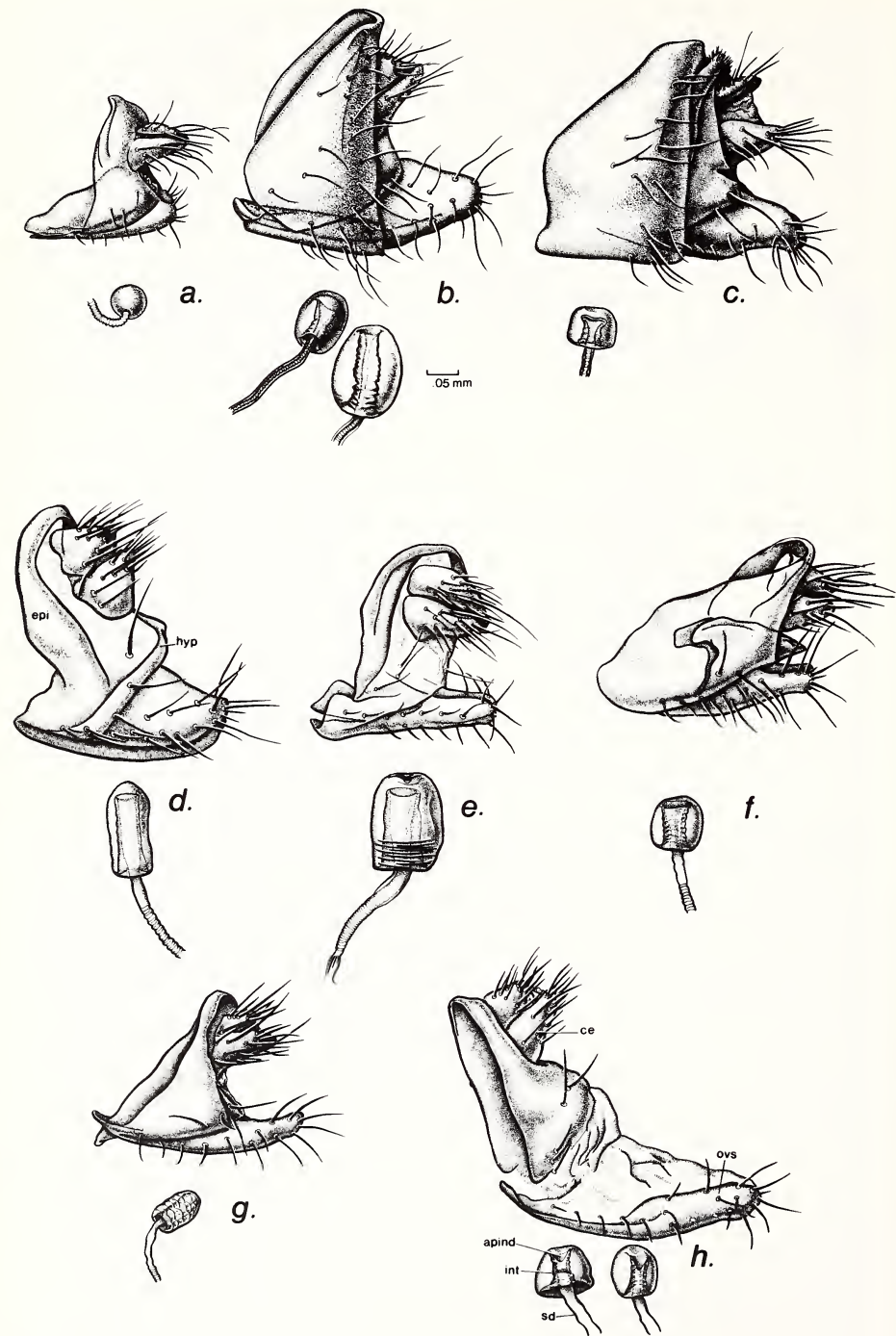
Chymomyza bicoloripes: Wheeler, 1957:103.

Since Malloch and Hendel described the habitus, I deal with it here only briefly and concentrate on the very diagnostic terminalia.

Description. Arista with 4–5 dorsal and 2 ventral rays. Orbitals in line with each other and with inner verticals. Eyes moderately pilose. Inner vertical setae longest, ocellars shortest setae on head. A large vibrissa subtended on each side by 6 smaller setae, their lengths about ½ that of vibrissa. Four subgenal setae and 10 postoculars per side of head. Six rows of acrostichal setulae. Male without pro- or mesothoracic femoral spines. Wings with distinct brown cloud over end of R_{4+5} extended to distal end of M or just distad; prominent infuscation over crossvein dm-cu. Wing measurements: C.I. = 1.18 (6♂♂), 1.30 (2♀♀); 4-V index = 1.95 (6♂♂), 1.87 (2♀♀); 4-C index = 1.38 (6♂♂), 1.28 (2♀♀). Other measurements: HW/ThL = 0.80 (6♂♂), 0.73 (2♀♀).

Female terminalia relatively small, oviscapae blunt, with 5–6 short, curved setae/sensilla on ventral margin and evenly spaced from each other. Apex with 2 short, peg-like sensilla and 3–4 longer setae, the 2 thick ones resembling sharp scales. Spermathecae small, spherical, heavily sclerotized, without an introvert.

Male terminalia large, most portions elongate. Cercus and dorsal margin of epandrium elongate in profile. Dorsolateral surfaces of epandrium with 9–10 strong setae



per side. Thirteen to 14 short prensisetae per surstylus. Ventral epandrial lobe narrow and very elongate, length about twice that of cercus. Strong, straight setae along its length, terminal ones best developed. Distiphallus enlarged, scoop-like, and with curved apical margin. A very elongate hypandrium not ventrally cleft. Several processes lateral to aedeagus present: A well-developed paraphysis with 5 sharp sensilla on dorsal surface; gonopod reduced and with thin apical seta and 3 evenly spaced setae of equal length on dorsal margin; the most lateral process, between ventral epandrial lobe and gonopod, forming a direct extension of that part of hypandrium connecting to gonopod. This thin lobe probably a gonopod derivative. Very little curvature in main shaft of basiphallus, aedeagal apodeme long and without lateral flanges.

Material examined. Besides the two type specimens mentioned above, the following were also studied: COSTA RICA: La Francia, Goodyear Estate, VI-1-52, J. B. Carpenter, 52-6587 (USNM). GUYANA: Tukeit (Falls), 20.VII.1911, "L.4.b." on back of label (1♀) (AMNH). PANAMA: Almirante, Bocas del Toro Pr., F. S. Blanton, Jan. 1953 (1♂), and Nov. 1952 (1♂) (USNM); Darien Province, Jaque, 28 July 1952, F. S. Blanton (2♂♂) (USNM). TRINIDAD: Arima, Blanchisseuse Rd., 2,000', 28-31 Jan. 1982, M. S. Adams (1♀) (CUIC). VENEZUELA: Bolivar, Rio Karui, 16 mi N Kavanayen, 1,000 m, 10-11 Aug. 1970, R. E. Dietz (1♂) (USNM).

Comments. This species is a very derived member of the *guyanensis-diatropa* lineage. Besides other specimens that are in the USNM collection from Turrialba, Costa Rica, Wheeler (1957) mentioned that he had seen specimens collected on Barro Colorado Island, Panama, "off a fresh-cut log" and at Villavicencio, Columbia. This species is widespread throughout Central America and probably tropical areas of South America but it is not known to reside on any of the Antilles.

***Chymomyza procnemolita*, new species**

Figs. 5, 13b, 14A, 15b, 17

Description. Male head generally narrow, broader in some specimens than others. Heads in both sexes very flat and with elongate profile. Arista with 3-4 dorsal branches (terminal one very small) and with 2 ventral ones. Ocellar triangle varying from slightly darker than yellow head color to dark brown. Inner vertical slightly mediad of line extending from anterior to posterior reclinate orbital setae. Anterior reclines level with dorsal margins of scapes. Proclines lying $\frac{1}{2}$ distance between anterior

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Fig. 13. Female terminalia (lateral views) and spermathecae, all to the same scale. Orientations of some structures, especially the epiproct in relation to the hypoproct, were not standardized. They are shown here mostly as a reference for the differences in relative sizes of spermathecae, oviscapes, and associated sclerites. a. *C. bicoloripes*; b. *C. procnemolita* (left spermatheca from Trinidad specimen, right one from Costa Rica); c. *C. diatropa*; d. *C. aldrichii*; e. *C. mycopelates*; f. *C. microdiopsis*; g. *C. procnemoides*; h. *C. exophthalma* (left spermatheca from Panama specimen, right one from Peru). The structures are arranged in order from blunt (a) to pointed (h) oviscapes. The oviscape of *C. exophthalma* is shown entirely everted. Abbreviations: apind, apical indentation; ce, cercus; epi, epiproct; hyp, hypoproct; int, introvert; ovs, oviscape (=sternite 8); sd, spermathecal duct.

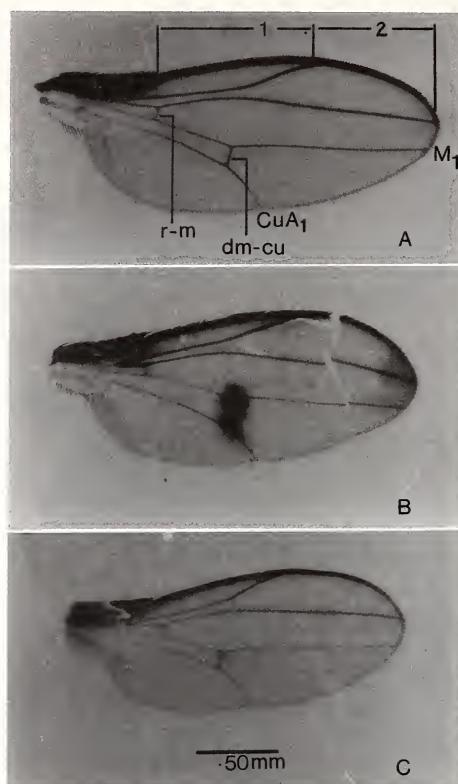


Fig. 14. Wing photographs of A. *C. procnemolita* female; B. *C. bicoloripes* female; C. *C. microdiopsis* male. Measurements: Costal Index (C.I.) = segment 1/segment 2; 4-V index = length from dm-cu to end of M_1 /length from r-m to dm-cu; 4-C index = segment 1 length/length of segment from r-m to dm-cu.

and posterior reclimates, or slightly closer to anterior reclimates. Proclimates terminating at inner margins of scapes. Strong, forward-projecting vibrissa subtended on each side by 4–6 setae about $\frac{1}{2}$ its length. One strong genal and 1 thinner but equally long subgenal seta per side. Eleven to 14 postoculars (usually 12) present per side; always 2 paraverticals per side, their length less than twice that of postocellars. HW/ThL = 0.94 (8♂♂), 0.91 (9♀♀); 2♂♂ from Panama with HW/ThL = 0.95 and 2♀♀ = 0.90; ThL = 0.76 (10♂♂), 0.86 (11♀♀).

Female terminalia diagnostic. Broad oviscap, apically truncate with 4 long and 3 shorter apical setae. Spermathecal height $1.5\times$ that of width. No apical indentation, but introvert extending entire length of capsule. Half of introvert near spermatheca opening with ribs, and, in a Costa Rican specimen, the ribs extended to introvert apex but here less distinct. Costa Rican specimen with enlarged spermatheca, oviscap similar to that of figured Trinidad specimen (Fig. 13b).

Like some other species in group, male terminalia varying in amount of vestiture on ventral epandrial lobes and gonopods and of microtrichia on distiphallus. Cercus

broadly rounded in profile and each surstylus with 7–8 prensisetae of moderate length. About 8 fine setae along ventral portion of cercus underneath epandrium. Ventral epandrial lobe with 3 strong, very long apical bristles and 15–20 shorter ones over remainder. Sparse microtrichia sometimes present on dorsal surface of lobe. Two setae on internal wall of each side of epandrium, lengths about that of epandrial lobe setae. Distiphallus well sclerotized but slightly membranous ventrally, lateral knob present. Distiphallus apex bare or with very sparse microtrichia. Main endophallal shaft extended out straight from aedeagal apodeme, then bent sharply ventrad and lying parallel with gonopodal apodeme. Paraphyses distinct, but still just raised portions of gonopod bases, each with 2–3 short, straight sensilla. Gonopod with dense vestiture of microtrichia, especially on dorsal surface. Ventral margin of hypandrium short and uncleft. No lateral flanges on aedeagal apodeme.

Holotype. ♂, TRINIDAD: Arima, Blanchisseuse Road, 2,000', 28–31 January 1982, Morton S. Adams (USNM).

Paratypes. COSTA RICA: La Suiza, July 1926, Pablo Schild (1♀) (USNM). PANAMA: David, Chiriqui, 2,200', 24 July 1964, A. Broce, light trap (1♂, 2♀♀) (USNM). TRINIDAD: Arima, Blanchisseuse Rd., 2,000', 28–31 Jan. 1982, M. S. Adams (4♂♂, 11 ♀♀) (USNM, CUIC).

Etymology. Gr., derived from *Chymomyza procnemoides*, as “plain procnemoides,” or, literally, “plain swallower.”

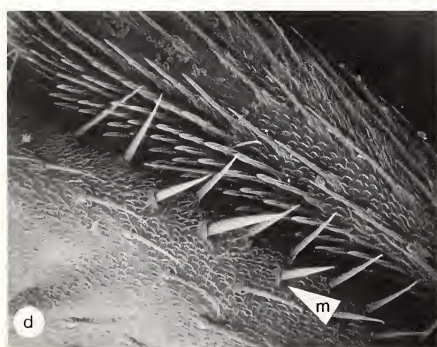
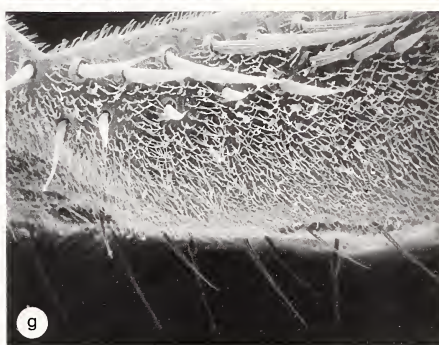
***Chymomyza diatropa*, new species**

Figs. 3, 13c, 17

Description. Male head broadened slightly to not at all. Three dorsal, 2 ventral arisal rays. Proclinate extended to middle of pedicel: bases slightly forward $\frac{1}{2}$ distance between 2 reclinate and just lateral to fronto-orbital sulcus. Posterior reclinate lying $\frac{1}{2}$ distance between anterior reclinate and inner vertical. Anterior reclinate lying far forward: its level on face in line with middle of scapes, sometimes to almost dorsal margin of scapes. Anterior margin of face with dark brown area extended slightly past distal end flagellomere I. Five strong subvibrissal setae, their thickness at most $\frac{1}{2}$ that of vibrissa. Moderately dense, short eye pilosity. Eight to 10 postocular setae per side of head, 2–3 paravericals (2 always between verticals). Inner verticals and posterior reclinate orbitals longest setae on head; proclinate and genals shortest.

Eight irregular rows of acrostichal setulae. Anterior scutellars in line with dorso-centrals. One large postpronotal seta. Thorax uniformly orange to amber. Prothoracic coxa with 5–6 setae, femur with 7–9 long spines (equal to or greater in length than femur width) in medial row, lateral row with 10 straighter and stouter spines. Mesothoracic coxa with 2 forward-projecting setae, metathoracic coxa with 1–2 setae. Wing measurements: C.I. = 1.09 (5♂♂, Guyana), 1.08 (3♂♂, Costa Rica), 1.32 (1♂, Venezuela), 0.99 (3♀♀, Guyana); 4-V index = 2.62 (6♂♂, Guyana), 2.42 (3♂♂, Costa Rica) and 2.52 (3♀♀, Guyana); 4-C index = 1.90 (6♂♂, Guyana), 1.70 (2♂♂, Costa Rica) and 1.86 (3♀♀, Guyana). Other measurements: HW/ThL = 1.07 (9♂♂, Guyana), 0.80 (5♂♂, Costa Rica), 0.85 (5♀♀, Guyana); ThL = 787 μ m (16♂♂), 790 μ m (5♀♀).

Male terminalia, but not female, somewhat variable. Eight to 9 prensisetae per surstylus, cercus apically rounded but ventrally flat in profile. Ventral epandrial lobe



straight or slightly upcurved, bearing 20–30 long setae (greater in length than width of ventral epandrial lobe), some hidden beneath epandrium. Hypandrium deeply cleft ventrally. Gonopod always broad laterally, apex sometimes twice the height of base. Gonopod with 2 scale-like setae laterad, 4–7 thinner dorsal setae. All gonopod setae upright, projected dorsad. Gonopod sometimes devoid of microtrichia, but usually with varying amounts on dorsal surface (perhaps some rubbed off during mating). Endophallus profile not emarginate, but wrinkled proximad due to membranous surface. Ventral tooth of phallapodeme absent, or, when present, minute and very close to crotch of basiphallus and aedeagal apodeme; aedeagal apodeme short, narrow in profile. Paraphysis rudimentary, a lump on medial surface of gonopod, with 3 short, sharp sensilla. Distiphallus without a lateral knob and without vestiture. Female with intermediately-broadened oviscape curved slightly downward. Epiproct with many fine setulae on dorsal surface. Spermatheca as high as broad; introvert structure invariant.

Holotype. ♂, Tukeit, British Guyana, 20.VII.1911. Back of label: “L.4.b.” (AMNH).

Paratypes. 9♂♂, 5♀♀, Tukeit, British Guyana, 20.VII.1911. Also on the back of each label is written “L.4.b.” (AMNH).

Other material examined. COSTA RICA: Turrialba, XII-6-52, J. B. Carpenter (on *Hevea braziliensis* tap panels) (5♂♂) (USNM). DOMINICA, WEST INDIES: Clarke Hall, July 1964, T. J. Spilman (light trap) (1♀); Bells, 20 September 1965, D. L. Jackson (1♂) (USNM). ECUADOR: Puyo, 16 May 1977, P. J. Spangler & D. R. Givens, #51 (1♀) (USNM). PANAMA: Chiriqui, Chiriqui Viejo Riv., El Volcan, 5,280', 22 July 1966, A. Broce (light trap) (1♂) (USNM). UNITED STATES: Miami, Florida, 28 January 1969, J. C. Buff (light trapping) (1♂) (USNM). VENEZUELA: Aragua, Rancho Grande, 1,100 m, I. '66, S. S. & W. D. Duckworth (1♂) (USNM).

Etymology. Gr., “variable,” because the morphological variation found in this species exceeds that of any other in the group.

Comments. This is the most widespread and variable of the neotropical species. Although some specimens seem different enough from the main sample of Guyana specimens as to perhaps represent different species (i.e., the Venezuela and Panama specimens), the male terminal show an obvious overall similarity. The species is distributed from southern Florida and probably most of tropical Mexico, throughout the Greater and some Lesser Antilles, and probably to the southern margin of the Amazon basin. The type-locality, Tukeit, British Guyana, probably refers to Tukeit Falls in the Mazaruni-Potaro District of Guyana (5°13'S, 59°25'W).

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Fig. 15. Scanning electron micrographs of some male *Chymomyza* prothoracic femora (550×, 5 kV), showing the variations in spine structure, number, and positions. a. *C. bicoloripes* (Bolívar, Venezuela); b. *C. procnemolita* (Arima, Trinidad); c. *C. guyanensis* (Tukeit, Guyana); d. *C. microdiopsis* (Santa Clara, Cuba); e. *C. aldrichii* (Pacific Grove, California); f. *C. procnemoides* (Lapeer Co., Michigan); g. *C. amoena* (Guelph, Ontario); h. *C. mycopelates* (La-Francia, Costa Rica). Abbreviations: m, medial spine row; p, fine ventral pollinosity; v, ventral portion of femur; vr, ventral spine row.

***Chymomyza jamaicensis*, new species**

Figs. 4, 17

Description. Head yellow, anterior margin face dark brown and extended to about distal tip of flagellomere I. Arista with 3 dorsal and 2 ventral branches. Proclimates strongly convergent, ends almost touching. Inner verticals lying mediad of line extending through reclinate setae. Position of anterior reclinate below line extending across dorsal margin of scapes. Seven subvibrissal setae per side of head. Paravertical setae longer than twice postocellar length. Eyes bare, dorsal portion extended outward on elongate fronto-orbital plate with facial portion unmodified and here distance separating eyes about equal to frontal vitta width. Inner vertical seta longest, proclimates shortest ones on head. Pleura chocolate brown, gradually lightened posteriad; metakatepisternum light (same color as coxa), notum and scutellum red-brown, and subscutellum same color as pleura. One large postpronotal seta, 8 rows of acrostichals. Forecoxa with 6 prominent setae. Forefemur with 15 spines in medial row (ventral row obscured). Mesothoracic coxa has 4 and metathoracic coxa with 1 seta. All portions of meso- and metathoracic legs orange. Wing measurements: C.I. = 1.07, 4-V index = 2.98, 4-C index = 2.02. Other measurements: HW/ThL = 1.29, ThL = 880 μ m.

Male terminalia with cercus apically pointed but dorsally rounded in profile. Numerous fine setae on ventral surface of cercus. Ventral epandrial lobe straight, ending bluntly but not knobbed. Ten prenisetae per surstylus, dorsal margin of epandrium short. Well-developed paraphysis bearing 3 apical, sharp sensilla. Distiphallus large, curved sharply dorsad at apex, and ventral margin with 6 blunt serrations and large knob between them and basiphallus. Distiphallus devoid of microtrichia. Gonopod base narrow, distal portion with 2 large, apical scale-like setae and 4 smaller, equal-sized setae medially. Gonopodal apodeme robust. Basiphallus high in profile and without lateral flanges. Gonopod devoid of microtrichia.

Holotype. ♂, JAMAICA: Hardware Gap, 4,000', VII-6-66, Howden and Becker (CNC).

Etymology. Latin, "from Jamaica," in regard to the type locality.

Comments. This description is based on the holotype, which is the only specimen known for the species.

***Chymomyza guyanensis*, new species**

Figs. 8, 15c

Description. Head narrow, face elongate. Inner margins of eyes meeting outer margins of flagellomere I. Arista with 3 dorsal and 2 ventral branches. Proclinate orbital setae terminating at middle of pedicels. Head yellow, except for darkened ocellar triangle. Fronto-orbital plates extended slightly beyond proclinate orbitals. Twelve to 16 postocular setae per side of head; postocellars minute. Eye pilosity short and sparse, especially anterior part of eye. Anterior reclinate, posterior reclinate, and inner vertical setae in line with each other on each side of head. Proclimates much closer to anterior reclinate than to posterior reclinate. Anterior reclinate situated above line extending across dorsal margins of scapes. A strong, forward-projecting

vibrissa subtended on each side by 4–6 equally thick, shorter setae. Two thin, straight genals, 2 paravericals, length of latter about equal to distance between inner and outer vertical setae.

Eight rows of evenly spaced acrostichal setulae. Anterior scutellar setae in line with dorsocentrals. Length of lateral prescutellar setae only about twice that of acrostichals. Prothoracic coxa with 4–5 heavy setae and numerous fine ones on medial surface. Sixteen straight, sharp spines in lateral row on male prothoracic femur and about 23 longer ones of similar shape in medial row. Fourteen evenly spaced finer setae on lateral margin of ventral pollinosity. Hind tibiae dark brown, other parts of legs, including femora, lighter and unicolorous with pleura and notum. Wing measurements: C.I. = 0.96 (10♂♂), 1.14 (2♀♀); 4-V index = 2.55 (10♂♂, 2♀♀); 4-C index = 1.80 (10♂♂, 2♀♀). Other measurements: HW/ThL = 0.83 (9♂♂, 2♀♀).

Oviscape and spermathecae very similar to those of *C. diatropa* and not figured. Gonopods and distiphallus variable. Cercus rounded in profile, surstylus with 8–9 prenisetae, ventral epandrial lobe invariant and with short ventral setae projecting ventrad (their lengths about equal to lobe width) but gradually longer proximad. Dorsal portion of aedeagus connecting distiphallus to epandrium loose and membranous. Apex of distiphallus membranous, apparently eversible: internal sac visible in specimens with an elongate aedeagus, in specimens where apical microtrichia unapparent, aedeagus also appearing unevered. When unevered, distiphallus not curved strongly dorsad as figured. Gonopods always with 2 strong, scale-like, lateral setae and 2 thinner ones on dorsal margin. Variable vestiture, primarily on dorsal margin of gonopod and sometimes reduced to just 8 or 9 microtrichia. Paraphysis a small lobe on medial surface of gonopod with 3 slightly curved, sharp sensilla. Hypandrium short, ventral margin slightly cleft or uncleft. Aedeagal apodeme triangular and high laterally, apex bearing lateral flanges.

Holotype. ♂, Tukeit, British Guyana, 20.VII.1911. Back of label has written on it "L.4.b." (AMNH).

Paratypes. 9♂♂, 1♀, all with same data as holotype.

Etymology. Latin, "from Guyana," in regard to the type locality.

Chymomyza albitarsis (Hendel, 1917)

Fig. 7

Zygodrosophila albitarsis Hendel, 1917:43. Holotype, ♂, PARAGUAY: Fichbrig, S. Bernardino. (NHMW).

Zygodrosophila albitarsis Hendel, 1917; Duda, 1927:69. (Discussed probable synonymy with *Chymomyza*.)

Chymomyza albitarsis (Hendel), 1917; Wheeler, 1981:33. (Synonymized *Zygodrosophila* with *Chymomyza* in world catalogue.)

Description. This description and the one by Hendel are based only on the type, the only specimen known for the species. Hendel's description of the head is needed since the head of the type specimen has been lost. Extracted from his description: head diagonally broadened, as in *Zygothrica*, 3 orbital bristles present, the uppermost one [the posterior reclinate seta] in the middle of the head and not curved above.

The foremost bristle [the anterior reclinate] lies beside the antennae. Bristles that are medially based [the inner verticals] are largest and also pointed forwards and inwardly.

The specimen is in a bad state owing also to the dense fungal mycelia covering the body. Thorax with 8 rows acrostichal setulae, light amber. One postpronotal seta. Prothoracic coxa with 5 strong bristles and numerous finer ones. Thirteen to 14 fine, straight spines in medial row on prothoracic femur, ventral row obscured. Wing measurement: C.I. = 1.34.

Terminalia most similar to *C. microdiopsis* and *C. jamaicensis*. Like these other 2 species, cercus apically pointed, ventral epandrial lobe bearing numerous short setae along length (especially apical-medial portion), ventral margin of hypandrium strongly cleft, and ventral knob present about $\frac{1}{2}$ distance along length of endophallal shaft. The species seems most closely related to *C. jamaicensis* because both possess a row of evenly spaced, short, fine setae on the flat ventral margin of the cercus. Unlike the geographically distant *C. jamaicensis*, though, aedeagal apodeme flared laterally, the ventral epandrial lobes distinctly knobbed, and distiphallus is quadrate and apically truncate. No vestiture on distiphallus and it possesses no ventral serrations.

Comments. I place this species in the *guyanensis-diatropa* lineage of the species-group due to the synapomorphies it possesses with *C. jamaicensis* as discussed above and, by judging from Hendel's description, because its head is probably modified in a manner similar to those of *C. jamaicensis* and *C. diatropa*.

IV. Phylogenetic relationships.

Although some species in the group are distinctive, patterns of genealogical relationships have not been easily discerned. Only 7 of the 43 synapomorphies were not in conflict with each other, which means that about 80% of the morphological characters are similar as a result of homoplasy (Fig. 16). Although this may be a consequence of the strict use of parsimony (and, particularly, its application to rapidly evolving characters such as those in the terminalia), I believe that this result is more a reflection that relationships among species in the group are truly obscure. Perhaps the time of species origins coincided so closely as to make the relationships among extant forms an essentially polychotomous one. Okada (1976) used a Mean-Cluster-Distance (MCD) proximity analysis and UPGA cluster analysis of a matrix of binary character states coded as either advanced or plesiomorphic. He did not indicate how the character polarities were decided, but it is interesting that he found 6 members in the *C. aldrichii* species-group to have relationships the least resolved among those in the 5 species-groups of *Chymomyza*. His analysis found the following pairs to be close relatives, but there were no apparent relationships among the 3 pairs: *C. aldrichii*-*C. coxata* Wheeler (the latter I have examined, and it appears to have a number of synapomorphies with several groups—my inclination is to agree with Wheeler [1952] in that its placement is uncertain), *C. mesopecta*-*C. procnemoides*, and *C. bicoloripes*-*C. laevilimbata*. *Chymomyza mesopecta* and *C. laevilimbata*, the 2 species not examined in this study, then, may be derived members of the large *diatropa-guyanensis* lineage, and they are not known to have broad-headed males. My analysis delineated 2 main lineages: the *mycopelates* and the *diatropa-guyanensis* lineages.

Table 1. Hypothesis of phylogenetic relationships for the *Chymomyza aldrichii* species-group (missing are *C. laevilimbata*, *C. mesopecta*, *C. albitarsis*, and *C. jamaicensis*: their affinities are discussed in the text). Apomorphies = "A," black dots on cladogram; Plesiomorphies = "P," circles on cladogram. The simplest hypothesis is provided by the branching diagram at the base of the character-state distribution matrix.

1. Interorbital width (A = broad; P = narrow).
2. Proclinate seta position (A = equidistant between reclines; P = closer to anterior reclinate).
3. Pleura color (A = darkened brown; P = light, thorax ground color).
4. Postalar seta length (A = shorter or equal in length to supralar; P = longer than supralar).
5. Male femoral spine length (A = undifferentiated between rows; P = lengths differ between rows).
6. Gonopod setae (A = undifferentiated; P = some are scale-like).
7. Spermathecal exterior (A = apex indented into introvert apex; P = apex smooth).
8. Procoxal seta number (A = less than 4; P = 6 or more).
9. Paraphysis seta number (A = more than 3; P = 2 or less).
10. Ventral margin of hypandrium (A = cleft; P = uncleft, margin even).
11. Eye pilosity (A = bare; P = developed).
12. Proclinate seta inclination (A = end is distant from middle of pedicel; P = ends at middle of pedicel).
13. Distiphallus vestiture (A = setose; P = glabrous).
14. Lateral aspect of distiphallus (A = pointed knob well developed; P = smooth lateral surface).
15. Facial coloration (A = dark brown area on anterior facial margin; P = unicolorous yellow or orange).
16. Spermathecal shape (A = length greater than width; P = length about equal to width).
17. Acrostichal row number (A = less than 8; P = 8 rows present).
18. Ventral margin of endophallal shaft (A = smooth, projections lost; P = projection developed).
19. Gonopod apex vestiture (A = microtrichia lost; P = microtrichia developed).
20. Ventral epandrial lobe seta lengths (A = undifferentiated; P = differentiated).
21. Lateral prescutellar seta length (A = $2 \times$ acrostichal setula length or less; P = greater than $2 \times$ acrostichal length).
22. Gonopod seta number (A = more than 1 scale-like seta; P = 0 or 1).
23. Paraphysis (A = rudimentary, inconspicuous; P = prominent).
24. Dorsocentral seta positions (A = in line with anterior scutellars; P = lateral to line extending from anterior scutellars).
25. Costal index (A = less than 1.20; P = greater than 1.40).
26. Apical ventral epandrial lobe setae (A = few, long; P = numerous, short).
27. Gonopod shape (A = pointed; P = rounded).
28. Notopleural seta lengths (A = differentiated; P = same).
29. Subvibrissal seta lengths (A = differentiated; P = homomorphic).
30. Minute orbital seta between proclinate and posterior reclinate setae (A = lost; P = developed).
31. Spermatheca size (A = small, 100 μ m diam. or less; P = 150 μ m or more).
32. Prensisetae number (A = reduced, less than 10; P = 11 or more).
33. Lengths of ventral epandrial lobe setae (A = long, more than $2 \times$ lobe width; P = short, length about = to lobe width or shorter).
34. Lunule coloration (A = bright yellow; P = head ground color).
35. Dorsal margin of epandrium (A = short, $\frac{1}{2}$ ventral length or less; P = long, about $\frac{3}{4}$ length of ventral portion).

Table 1. Continued.

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- 36. 4-C index (A = greater than 1.40; P = 1.40 or less).
 - 37. Lateral profile of male cercus (A = rounded; P = pointed).
 - 38. Distiphallus base (A = profile even; P = serrations developed).
 - 39. Male prothoracic femoral spine numbers (A = reduced, 15 or less in either row; P = numerous, 16 or more in either row).
 - 40. Paravertical seta sizes (A = short, less than $2\times$ length postocellars; P = $2\times$ postocellar length or greater).
 - 41. Distiphallus shape (A = rounded in profile; P = pointed or sharp).
 - 42. Vein dm-cu coloration (A = surrounding area hyaline; P = infuscated).
 - 43. Costal cell and adjacent regions (A = infuscated dark brown; P = no infuscation).
-

The former is based on the possession of glabrous eyes and the latter by the presence of a few, long apical setae on the ventral epandrial lobe of the male terminalia.

DISCUSSION

I. Neotropical diversity.

Thirteen of the 16 species of neotropical *Chymomyza* are members of the *C. aldrichii* species-group. The species-group is restricted to the New World and has 2 relatively derived nearctic members (*C. aldrichii* and *C. procnemoides*). It appears from my work that the *Chymomyza* fauna of Central and South America is probably twice that presently described. For this reason, and because of the paucity of specimens from different localities, the historical biogeography of *aldrichii* group species within the Neotropical Region must be left for future work. It does appear, however, that the group may have an African origin. According to Okada (1976), the *procnemis* species-group is the sister taxon to the *aldrichii* group. Of the 11 species in the former group (Okada, 1981; Wheeler, 1981), there is a polychotomous clade among them, all of them being derived species, and they include 4 African (primarily Ivory Coast) plus the New World species, *C. procnemis* (Williston). Distributions of most of the remaining, primitive species (sensu Okada, 1976) in that group are southeast Asian (India, Java, New Guinea, Philippines, Sumatra). Dating of an Africa-South America vicariance event would place the origin of the New World *aldrichii* radiation at about 75 million years ago, or in the late Cretaceous (Dott and Batten, 1971).

The other neotropical *Chymomyza* that are members of groups other than the *C. aldrichii* species-group are *C. mexicana* Wheeler (in the *C. costata* species-group) and, in the *procnemis* species-group, *C. pectinifemur* Duda and *C. procnemis*. *Chymomyza mexicana* is distinguished by its black body color, including the fore tarsi, and the latter 2 possess milky-white apical wing spots and a light body color similar to that of most *C. aldrichii* group members.

II. Breeding and feeding sites.

Chymomyza aldrichii species-group members are associated with wood, particularly injured and decaying portions. This is in strong contrast at least to the poly-

phagous species *Chymomyza amoena*, a common nearctic fly whose breeding sites have been relatively well surveyed. As adults, the *C. aldrichii* group flies feed on either the tree sap or a combination of this plus the bacteria, yeasts, and fungal hyphae and spores occurring in it that cause its natural decay. It is unclear on what portions of injured and decaying wood the larvae would feed, although, it can be assumed they use substrates similar to, but more restricted than, those used by adults.

These conclusions are based on several dozen specimens in the USNM that were found with labels referring to their food habits, plus some anecdotal notes both published and unpublished. In Washington state, 6 male *C. aldrichii* and a female were taken from a Douglas fir bolt (*Pseudotsuga menziesii*: Pinaceae) infested by *Trypodendron* and *Gnatotrichus*, and 2 more males and a female reared from the "galleries of *Trypodendron lineatum*." In Colorado, 4 male *C. aldrichii* and a female were reared from *Picea engelmanni* (Pinaceae), and 4 males and 3 females were captured on aspen (probably *Populus*: Salicaceae) trunk wounds. A single male of this species was taken in Idaho from *Pseudotsuga menziesii* (Pinaceae). Wheeler (1952) mentioned that numerous *C. aldrichii* in the collection at the University of Texas from the western United States were caught over peeled areas on the bark of aspen (*Populus*), fir (*Abies*) and Pine (*Pinus*), and the larvae of some from Minnesota were found in the bark of *Populus grandidentata* and *P. tremuloides*. Decaying logs of *Pinus alba* and *Populus tremuloides* are also mentioned as hosts, with *Betula alba* (Betulaceae) bark, by Teskey (1976). A female of *C. procnemoides* was taken in Virginia on "Tulip-poplar sap" (probably that of *Liriodendron*: Magnoliaceae).

The neotropical members of the group are likewise associates of trees, but as far as known only as adults. A male of *C. bicoloripes* in the USNM collection bears a label "on rubber [*Hevea brasiliensis*: Euphorbiaceae] tapping panel." This is supposedly one habit of *C. bicoloripes* in Costa Rica (Carpenter, 1954). The species to which Carpenter's account actually refers, though, is probably *C. mycopelates*: In the same collection is a large series of males and females, all of them captured in Costa Rica on *Ceratostomella* fungus (Conidiophoraceae) that was infesting the latex tapping panels of rubber trees. According to Carpenter's record, the flies not only passed up visiting nearby infructescences of *Fusarium* (Myxomycetes), but their attraction to *Ceratostomella* is probably a result of an odor produced by a specific combination of amyl acetate and butyl alcohol that is distinctive to the group of fungi to which this genus belongs. Five males in the USNM of *C. diatropa* were similarly caught in Costa Rica. In addition, the specimens of *C. exophthalma* that I collected in Peru were swept over cut logs and sawdust of a tree (family Lecythidaceae) in a tropical-moist inundation forest (Rio Tambopata Reserve, Madre de Dios). Unlike most other drosophilids in the area, these flies were not found by sweeping understory vegetation, or over macrofungal sporophores and fallen fruits and flowers. Broadhead (1984) discussed morphological traits associated with fungal grazing by adult Lauxaniidae. Although these *Chymomyza* show no obvious pseudotracheal modifications (i.e., prestomal teeth) nor an enlarged labella, as in most mycophagous lauxaniids, a gut content analysis would provide useful information as to the actual foodstuff.

The association of *C. aldrichii* group flies with certain woody tissues of trees is probably a specialization derived from a primitive polyphagous habit. *Chymomyza amoena*, for example, has been reared from various decaying fruits and plants such

as *Symplocarpus* (Araceae) spathes and broomrape (*Conopholis*: Orobanchaceae) in New York and from apples, pears, and crabapples (*Pyrus coronaria*: Malvaceae) in Michigan. It appears especially fond of walnut and butternut (*Juglans*: Juglandaceae) husks throughout much of its range, which are no doubt its natural hosts. Outgroup comparison, then, shows that there is also a predilection for woody, fibrous, and decaying plant tissues in several plant taxa. The only mention of larval morphology in the group is a habitus drawing of *Chymomyza aldrichii* by Teskey (1976, 1981).

III. Sexual dimorphism and behavior.

A. Head shape analysis: Interspecific comparisons.

Five ratios of 6 head measurements were calculated to determine the parts of the cranium involved in male head broadening among some of the species. The ratios, denoted also by their abbreviations in parentheses, were the following: total head width/total thorax length (distance from the anterior margin of the notum to the posterior apex of the scutellum) (HW/ThL), eye depth/head depth (ED/HD), total width of eyes/head width ($EW \times 2/HW$), frontal vitta width/head width (FVW/HW), and frontal vitta width/minimum interocular distance on the face (FVW/MID) (see Fig. 17 for the location of some of these structures). Also, log-transformed values of individual male head widths were plotted on log-transformed values of their thorax lengths (a convenient and accurate estimate of body size) for males of 8 species in order to determine the linear fit of head expansion as a function of overall body size.

1. Relative head widths.

For 8 species where enough male specimens could be measured, all had high, positive relationships between size and head width. How much the head width varied with respect to size, though, differed considerably among species. The slope of this relationship was steepest for *C. microdiopsis*, *C. diatropa*, *C. exophthalma*, and, curiously enough, for the narrow-headed species *C. procnemolita*. Among these species dramatic differences were found in relative head widths that were not accountable just to differences in size (Figs. 17, 18). *Chymomyza amoena*, *C. procnemoides*, *C. aldrichii*, and *C. guyanensis* head sizes differ less dramatically among differently-sized males. Table 2 provides a summary of the relationships for this allometric trait.

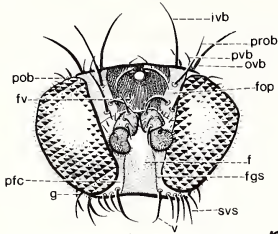
Chymomyza microdiopsis, *C. diatropa*, and *C. exophthalma* have the most pronounced sexual dimorphism for the trait, the males having relative head widths (HW/ThL) 1.39, 1.12, and 1.18 times that of the females, respectively. Males of the other species have heads 0.99–1.09 times that of the relative female (mean = 0.82) head width. Also, females of the broad-headed species have slightly broader heads than the females of normal-headed species.

2. The components of the broadened crania.

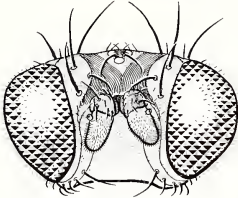
Except for *C. microdiopsis*, eye depth in relation to total head depth does not vary much among species (0.80–0.91), with *C. microdiopsis* having the shallowest eyes, and the remaining species varying from 0.87–0.91 for this trait. Little or no sexual dimorphism for this trait was found.

NARROW-HEADED FORMS

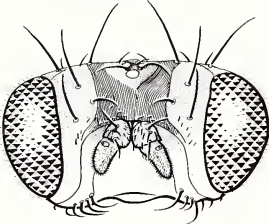
BROAD-HEADED FORMS



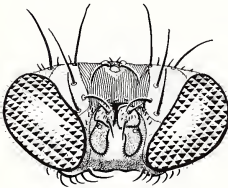
mycopelates



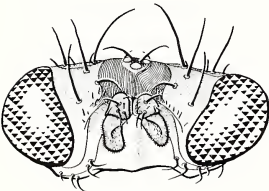
procnemolita



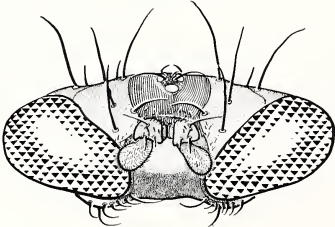
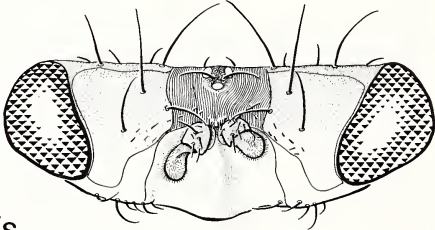
exophthalma



diatropa



microdiopsis



jamaicensis

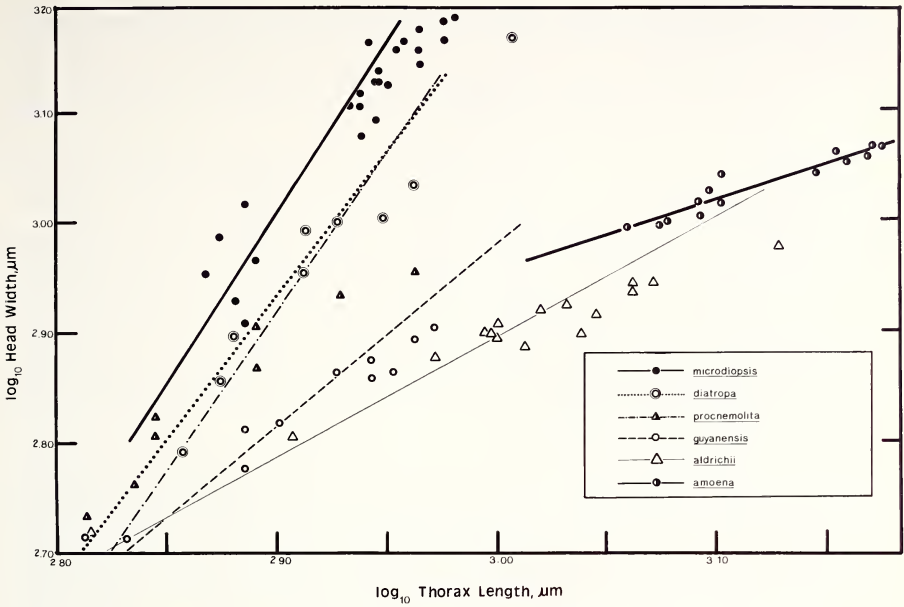


Fig. 18. Allometric relationships for male head widths as a function of body size (thorax length) for 6 *Chymomyza* species. Linear regression equations of the log-log plots are presented in Table 2.

Eye width varies considerably in relation to total head width among species. Two species having very narrow eyes, *C. microdiopsis* ($EW \times 2 / HW = 0.51$) and *C. exophthalma* (0.46), are also species with extreme-type males. The mean and range of values for this trait for other species is 0.75 (0.64–0.79). Females of *C. microdiopsis* (0.68) and *C. exophthalma* (0.64) also have significantly narrower eyes in relation to their head widths compared to other *Chymomyza* females (mean = 0.75, range = 0.71–0.84).

Since, in *C. microdiopsis* and *C. exophthalma* males, the relative frontal vitta width (FVW/HW) is not expanded, their broad heads are due to a lateral expansion of the fronto-orbital and parafacial plates (Fig. 17). Females of these species share the trait, but in them it is much less pronounced. FVW/HW varies from 0.26–0.44 for males and females with no obvious sexual dimorphism. The relation between eye separation and the role of cranial sclerites causing it can be seen even more dramatically as the

←

Fig. 17. Frontal view of some male *Chymomyza* heads, all to the same scale. Broad-headed forms (in the right column) and the narrow-headed form are shown for some species and were chosen to represent the range in the morphocline; for those species represented by only one form either the variation for head shape is unknown (*C. jamaicensis*) or insignificant. Abbreviations: f, face; fgs, fronto-genal suture; fop, fronto-orbital plate; fv, frontal vitta; g, gena; ivb, inner vertical bristle (seta); ovb, outer vertical seta; pfc, parafacial plate; pob, post-orbital seta; prob, posterior reclinate seta; pvb, post-vertical seta; svs, subvibrissal seta; v, vibrissa.

Table 2. Log₁₀-log₁₀ linear regressions of male *Chymomyza* head widths (μm) as a function of total thorax lengths (μm).

Species	Relation	r ²	N
	y = mx + b		
* <i>aldrichii</i>	0.76x + 0.61	0.90	16
* <i>microdiopsis</i>	2.00x - 2.78	0.81	24
* <i>diatropa</i>	1.22x - 0.61	0.32	9
* <i>guyanensis</i>	1.06x + 0.26	0.92	9
* <i>procnemolita</i>	1.48x + 1.40	0.94	11
<i>exophthalma</i>	1.73x - 2.12	0.74	5
<i>procnemoides</i>	0.63x + 1.20	0.77	9
* <i>amoena</i>	0.61x + 1.13	0.90	14

* Relationships are plotted in Figure 18.

ratio of FVW/MID, where this value is smallest for *C. exophthalma* (0.57) and *C. microdiopsis* (0.53), but averages 1.30 (1.11–1.50) for males of the other species. It is interesting that, even though the males have distended eyes, *C. diatropa* and *C. jamaicensis* still retain a relative interocular distance (MID/HW) about equal to that of “normal” species. These 2 species have, however, a lateral expansion of the fronto-orbital plates on the dorsal part of the head and the parafacial plates remain of normal size.

In conclusion, for species with males that are conspicuously broad-headed, either the absolute eye size has remained unchanged in comparison to close relatives (i.e., *C. exophthalma*–*C. microdiopsis*) or it has been enlarged by a lateral extension of each eye. Either the parafacial plates, or the eyes, but not both, and always the fronto-orbital plates have become laterally distended in the highly modified males. Females of the species having broad-headed males share the trait but for them it is much less pronounced. This suggests that bizarre, sexual modifications of *Chymomyza* heads (and probably those of some other Acalyprtratae) are dramatic accents to modifications that have occurred first in both sexes.

3. Phylogenetic considerations of broadened crania.

Because the females of *C. jamaicensis* and *C. albitarsis* are unknown, these species were not included in the cladogram in Figure 16. Based solely on the males, however, they seem closely related to *C. diatropa* since at least *C. jamaicensis* and *C. diatropa* have conspicuously darkened anterior facial margins and because the eyes are distended in the same manner for all 3 species. Were this the case, then the evolution of broad-headed males would have taken place at least twice in the *C. aldrichii* species-group: Once in the *diatropa-guyanensis* lineage, where males have expanded eyes, and again in the *mycopelates* lineage, where the modification is a result of the involvement of 2 sets of frontal sclerites. Other drosophilid genera with members having broad-headed males reflect the 2 modes by which *Chymomyza* heads have broadened. *Drosophila heteroneura* (Perkins), a Hawaiian species, has normal eyes lying on expanded fronto-orbital and parafacial plates (the facial plate, too, has been expanded). Five species of *Zygothrica* (Wiedemann), on the other hand, have males

whose eyes are distended very much like those of *C. jamaicensis* and *C. diatropa* but in some of these species the modifications are much more extreme. It is interesting that one broad-headed member of each of the 2 lineages is probably a Caribbean island endemic: *C. microdiopsis* on Cuba and *C. jamaicensis* on Jamaica.

B. Leg ornamentation and reproductive behavior.

Spines, which are found only on the males of most *Chymomyza* species, are derived from the finer setae distributed evenly over the leg integument. This is based on the observation that both types of integumental outgrowths have a socketed base and possess longitudinal striae (Fig. 15). Ventral to the spines is fine pollinosity (Fig. 15), which is derived from the microtrichia also distributed evenly over most of the cuticle but, here, it is in dense patches and stands erect. The spines can vary in number per row (7–21), thickness, length, shape (Fig. 15), and their location. *Chymomyza mesopecta*, for instance, has lost the profemoral spines and instead developed them on the mesothoracic femora in males. The spines always occur in 2 rows.

Other than the loss of profemoral spines in the males of *C. bicoloripes* and *C. mesopecta*, synapomorphies for the character complex are few. Even closely related species can differ greatly in spine morphology: *C. diatropa* has 8 medial and 10 ventral, long spines and *C. guyanensis* has 23 medial and about 16 ventral, somewhat shorter spines (Fig. 15). Male femoral spines must evolve, like the terminalia and heads, at rates much faster than the rest of the phenotype. Although the spines no doubt function in male courtship and/or mating, they are probably ineffectual during intermale aggression. This conclusion is based on some behavioral observations, as well as the fact that no patterns of spine development occur concomitant with changes in head shape, the latter being a trait well known in some Diptera where head-butting contests among males take place.

Several individuals of *Chymomyza exophthalma* were kept in glass culture vials on instant drosophila medium (Carolina Biological Supply Co.) on 10, 11 October 1984, in Tambopata, Peru, and their behavior was observed. Like most *Chymomyza*, especially for the males, individuals were found to move quickly about in rapid stop-and-turn motions reminiscent of phorids. The sprints extended for about 5–10 body lengths. Periodically while sprinting, and sometimes immediately upon stopping or just before turning, the forelegs were extended laterally to about 3 times the width of the body. This was done either as a single motion to 3 times consecutively, and was usually repeated rapidly (once every 5 to 10 seconds). Generally every time the legs were extended, the wings were simultaneously spread from between 90° to usually closer to 180° apart from each other. In unison, these motions gave the fly the appearance of swimming. Also, as the fly stopped to turn, it usually would “paw” the ground with 3–4 alternate strokes of the forelegs, then either “swam” or walked on.

During confrontations, which lasted between 4 and 16 seconds (7 observations), a pair would meet head-on and about ½ a body length apart. The meso- and meta-thoracic legs remained planted but the prothoracic legs were raised so that the tarsi were above the dorsal surface of the body. The legs were then lashed out against the opponents' tarsi (and perhaps other parts, such as the face) and, if the “standoff” escalated, each fly gradually raised itself higher from the substrate but to no more than twice the original stance height. Just prior to the “standoff” there often were

2–3 very rapid wing scissors, and during the “standoff” the wings were briefly outstretched about 100°. Male-to-male and male-to-female confrontations were similar, except that females did not scissor their wings. Flies never seemed to approach each other close enough so as to contact each others’ femoral spines during encounters, although they might have been able to detect them at least given the way they were exposed to the opponents. I observed no males butting heads, but more extended observation would likely prove more fruitful. Also, no courtship or mating was observed.

ACKNOWLEDGMENTS

Field work in Peru was funded by a research fellowship from the Harold E. Moore Fund of the Cornell University Bailey Hortorium. I was also able to peruse the USNM collection with the aid of a Smithsonian Short-term Visiting Fellowship. The Division of Biological Sciences at Cornell allotted me use of an SEM, and general services were provided by Hatch grant #NY(C)-139426 to Quentin D. Wheeler. Ruth Contreras-Lichtenberg made available to me a loan of Hendel’s type specimens: to her and the others previously mentioned I extend my gratitude. E. R. Hoebeke, J. Frank McAlpine, Wayne Mathis, and Stephen Nichols provided useful suggestions on the original manuscript. It is my pleasure to dedicate this work to Drs. Hans Burla and Hampton Carson, to honor them on their retirements.

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Received March 26, 1985; accepted July 29, 1985.